COLLEMBOLA AS POLLEN FEEDERS AND FLOWER VISITORS WITH OBSERVATIONS FROM THE HIGH ARCTIC[1]

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The literature is reviewed and observations are presented on the association between Entomobrya comparata *Folsom (Entomobryiidae) and* Lesquerella arctica *(Wormskjöld) S. Watson (Cruciferae) in northern Ellesmere Island. Collembola can feed directly on pollen from flower anthers. Collembola which visit flowers may be associated with those upon which they are inconspicuous because of their colour.* E. comparata *appears in the corollas of* L. arctica *flowers during a short "sensitive period" in its life history. It seems that the ameliorated thermal regime of the flowers may hold* E. comparata *and, combined with a rich source of nutrients, permit more rapid metabolism and greater activity than in hostile ambient arctic (or alpine) conditions.* L. arctica *is not dependent on arthropods for cross-pollination, so that* E. comparata *plays no significant role in the fertilization of the one plant with whose flowers it is known to be associated.*

Some Collembola species are certainly catholic in their choice of food, whereas others are much less so, although satisfactory evidence regarding the food preferences of any species is virtually lacking (Christiansen, 1964). Bödvarsson (1970) has recently given a comparative account of the gut contents of a few soil-inhabiting species, but there is no evidence of specific food preference. Pollen is one of the materials ingested by Collembola, and there are numerous references to this in the literature, although most of them are second-hand. Original observations are few and there is little published evidence that Collembola obtain pollen directly from the anthers of flowers, although this has been implied by Handschin (1919, 1924, 1926): "Von Pollen dürften sich . . . die Anthophilen ernähren"; "Blütenbewohner sind Pollenfresser"; and ". . . auf den Antheren der offenen Blüten [alpiner Ranunculaceen] . . .". There are a few published records of known pollinivorous species found in flowers (Carl, 1901; Handschin, 1919, 1924, 1926; Folsom *in* Brittain, 1924; Macnamara, 1924; Strebel, 1932, Folsom, 1933, 1934), but this does not necessarily mean that the Collembola feed directly on pollen from the anthers, although, in some instances, this appears to be so. Most records of pollen feeding, if they indicate the source of pollen found in gut examinations, suggest or imply that the pollen is wind-borne. Agrell (1941:56) makes a point of stating that, although *Bourletiella (Deuterosminthurus) repanda* (Ågren) [as *D. bicinctus* (Koch) f. *repanda*] clearly feeds on the pollen of *Trollius europaeus* Linnaeus (Ranunculaceae) in Swedish Lapland, he found the species only under leaves. *B. repanda* was not common, but found its optimum conditions in *Trollius* meadows.

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Agrell (1941: 127) also observes that, although *Entomobrya nivalis* (Linnaeus) and *Lepidocyrtus lanuginosus* (Gmelin) are both known to feed on pollen, when living in a macrophytic habitat they seldom had pollen in their intestines; these usually contained plant epidermis and parenchyma cells. This confirms his statement (p. 126) that a given species may feed mostly on one thing (e.g., fungus) in one locality, and chiefly on another (e.g., litter) in a different place. There seems to be no evidence that any species of Collembola so far observed is solely dependent upon pollen for its nutrition (see also Gisin, 1948), nor that any pollen-feeding species is dependent for its food supply upon the visiting of flowers, although Handschin (1924) suggests that this may be so for *Bourletiella lutea* (Lubbock).

LITERATURE REVIEW

The early works on pollination by Müller (1873) and Knuth (1898-1905, 1906) – like later works, such as those of Vogel (1954) and Faegri and Pijl (1966) – make no mention of Collembola. Neither does the classic work of Lubbock (1873) on Collembola mention pollen feeding by these animals. And although Linnaniemi (1907, 1912) in his monumental study of the Finnish Collembola mentions a number of species associated with vascular plants, he does not indicate that any of them visit flowers or consume pollen.

One of the earliest records of Collembola visiting flowers is that of Carl (1901), who records *Sminthurus luteus* [= *Bourletiella lutea*], in numbers of 10 to 25 together, from the involucres of woolly, high Alpine Compositae in Switzerland. He refers particularly to *Leontodon taraxaci* (Allioni) Loiseleur-Deslongchamps [= *L. montanus* Lamarck] and believed that the Collembola sought refuge from the cold. He also suggested that the glandular hairs might serve as food, but no mention is made of the inflorescence proper, or of pollen. Doflein (1914: 92, 244), in discussing the food of snow and ice fauna, indicates that the 'snow-flea', *Degeeria* [= *Entomobrya*] *nivalis*, and the 'glacier-flea', *Desoria glacialis* Nicolet [= *Isotoma saltans* (Nicolet)], feed on debris, mainly pollen, especially, it seems, of conifers, but gives no direct evidence for this. Schött (1917) provides one of the earliest positive references when he mentions that, in South Australia, the intestines of many specimens of the 'Lucerne flea', *Sminthurus viridis* (Linnaeus) var. *medicaginis* Schött, contained pollen grains of dicotyledonous plants, although the principal gut contents were hyphal remains and spores of ascomycetes.

Handschin (1919) mentions that Collembola are found, among other places, on the flowering parts of plants, and states that 'anthophiles' must feed on pollen, instancing *Bourletiella lutea* and *B. pruinosa* (Tullberg) [? = *B. signata* (Nicolet)]. Both species are found in numbers up to 50 together in flowers of the European (Alpine) *Ranunculus glacialis*. The association between these Collembola and the flowers was so constant that he could predict the presence of the animals from that of the flowers. In a footnote, Handschin notes that, in glasshouses, *Entomobrya spectabilis* Reuter lives in orchid blooms and that it is found almost exclusively at flowering time. Handschin (1924) notes that *Bourletiella lutea* is always found in the blossoms of *Ranunculus glacialis*, so constantly in fact, that an interrelationship between plant and animal might be postulated. Apparently this collembolan seems to Handschin to be specialized to alpine and snowfield macrophytes and to seek out flowers of all suitable low plants, which differ according to locality. He states that there is but one conclusion to be drawn: that this animal finds its source of nourishment in the reproductive organs of higher plants and seeks out suitable localities to this end. The question of whether the Collembola play a part in pollination is left open. In addition to the two species previously recorded in *Ranunculus glacialis* flowers, Handschin (1924) also lists *Bourletiella (Deuterosminthurus) repanda* [as *D. bicinctus repandus*], *B. (D.) pallipes* (Bourlet) [as *D. bicinctus pallipes*] and *Lepidocyrtus lanuginosus* [as *L. l. albicans* Reuter]. From the flowers of *Anthyllis vulneraria* Linneaus (Leguminosae) he records *B. lutea* and *Entomobrya nivalis* [ab.] *immaculata* Schäffer; and from *Campanula barbata* Linnaeus (Campanulaceae), *B. pruinosa* [? = *B. signata*]. With reference to the Alpine 'glacier-flea', *Isotoma saltans*, he indicates that coniferous pollen filled the intestines of this species, all of the pollen grains being intact.

Macnamara (1924) states that *Sminthurus hortensis* Fitch [? = *Bourletiella signata*] occurs in dandelion [*Taraxacum*, Compositae] heads in Canada [Ontario], but he does not indicate that it feeds on the pollen from this plant. Folsom (*in* Brittain, 1924) makes the same observation for the United States of America. Although Macnamara says that some pollen-feeding species go directly to flowers (his examples being the ones already cited), he also mentions that *Isotomurus* [as *Isotoma*] *palustris* (Müller) and *Sminthurides* [as *Sminthuris (sic)*] *aquaticus* (Bourlet) are species that occur on the surface of pools and streams (where they often pick up diatoms and desmids) and which, in spring, feed largely upon wind-borne pollen of conifers.

Handschin (1926) reviews what was known of the feeding habits of Collembola up to that time. He makes several references to Collembola inhabiting flowers and mentions that the species he reported to occur on the anthers of open blossoms of Alpine Ranunculaceae are now and again found, fortuitously, in *Campanula* bells and in Compositae. The same author (Handschin, 1929) mentions that *Deuterosminthurus bicinctus* [presumably referring to *Bourletiella (D.) repanda*] lives largely in flowers and on plants, and reiterates his earlier statements.

Steinböck (1931) repeats earlier statements and quotes Keller (1911) as saying that the 'Gletscherfloh' [*Isotoma saltans*] utilizes tiny fragments of animals and plants for food when conditions are adverse, although no specific mention is made of pollen. Steinböck agrees that *I. saltans* feeds on conifer pollen and wind-blown plant detritus particles, but showed that it would not feed upon the dried remains of spiders or on other animal debris deposited in the icy heights by storm winds; nor did he believe that pollen grains play an essential, or even always an important role in the diet. *I. saltans* apparently has a distinct liking for chocolate on such rare occasions as this may be proferred! Steinböck (1939) emphasizes his earlier observations that *I. saltans* is not dependent upon conifer pollen for food, although it will feed on this, but largely consumes other materials, particularly algae in the form of "Kryokonit", or "Gletscherschlamm", and not small wind-blown insects and other small creatures as indicated by earlier authors (he cites [Taschenberg *in*] A.E. Brehm's 4th Edition of [Illustriertes] Tierleben, which we have not consulted).

Strebel (1932) also refers to pollen feeding by Collembola and mentions that *Bourletiella* (including *Deuterosminthurus*) and *Sminthurus* species are pollen feeders. His material of *B. (D.) repanda*, collected off grasses, contained large quantities of unbroken pollen grains, but he observes that it still remains to be determined whether the species feeds exclusively on pollen. His observations thus agree with those of Agrell (1941) already referred to. Strebel (1932) also mentions pollen in field-collected *Sminthurus viridis* (quantities of grains, mostly whole, some broken) and *Lepidocyrtus cyaneus* Tullberg (unbroken grains). He notes that *Folsomia fimetaria* (Linnaeus) occurred in the flowers of the house plant *Aspidistra elatior* Blume (Liliaceae) and that the intestines were filled with broken pollen grains. Pollen also adhered to the bodies of the animals so that Collembola could conceivably play a role in the pollination of *Aspidistra*. It may be noted that *F. fimetaria* is a soil-dweller, but the flowers of the plant are unusual in that they occur on the surface of the ground.

Folsom (1933, 1934) repeats his earlier statement (*in* Brittain, 1924) that, in North

America, *Bourletiella hortensis* [? = *B. signata*] is common on the flowers of dandelion [*Taraxacum* (Compositae)]. He adds (Folsom, 1934) that it devours pollen there. Ritchie (1935) observed that, under conditions of scanty and irregular rainfall, an undescribed species of *Drepanocyrtus* [probably nr. *D. flavovirens* (Börner)] may damage the blossoms (and kill minute fruits) of coffee [*Coffea* sp., ? *C. arabica* Linnaeus (Rubiaceae)] in Tanganyika.

Agrell (1941) mentions that Lapland sminthurids which normally live in macrophytic vegetation may have gut contents consisting almost exclusively of unbroken pollen grains. He refers, it seems, mainly to *Bourletiella (Deuterosminthurus) repanda* (see above); *Entomobrya nivalis* and *Lepidocyrtus lanuginosus* are the other pollen feeders mentioned. Kos (1944) reported similar findings in respect of the Balkan 'glacier-flea' ["triglaver schwarzen Isotomen", referred to *Isotoma nigra* Kos and subsequently identified (Paclt, 1956) as *I. kosi* Paclt = *I. kosiana* Bagnall] to those of Steinböck (1931) for *I. saltans*. Gut contents included mechanically undamaged pollen grains, probably of *Pinus mughus* Scopoli, together with other plant and fungous material.

Gisin (1947) mentions that the gut contents of Collembola may include pollen grains, and illustrates part of the intestine of a sminthurid – by implication, *Sminthurides pumilis* (Krausbauer) – containing collapsed pollen grains, spores and mineral matter. The same author (Gisin, 1948) remarks that the principal source of food for what he terms epigeic Collembola, is pollen, and that lactic-acid microscope preparations reveal in the gut the presence of various kinds of pollen grains, which are sometimes entire, sometimes fragmented or shrivelled, but that monophagy is unknown in Collembola.

Works by Denis (1949), Kühnelt (1950, 1957, 1961), Maynard (1951), Sedlag (1953), and Bellinger (1954), add nothing new. A brief general discussion of pollen feeding by Collembola is given by Paclt (1956). He lists *Bourletiella, Sminthurus, Katianna* and *Parakatianna* as plant dwellers and indicates that species belonging to most of these genera are known also as pollen feeders, although, so far, we have been unable to find any published reference to the habit in the last two genera. Species of *Folsomia* and *Lepidocyrtus* are also said to be known to consume pollen (*cf.* Strebel, 1932). Handschin's (1926) observations (above) are referred to, and it is considered unproven that any Collembola, including *Isotoma saltans*, can obtain all their food requirements from pollen grains (or the spores of higher fungi). Paclt observes, however, that if they cannot do so, one must enquire how they obtain their nutriment if the gut is filled only with pollen (or spore masses). He concludes that the possibility has been suggested that 'glacier-fleas' (*Isotoma saltans* and *I. kosi* [= *I. kosiana*]) may sometimes feed on animal matter, but that Steinböck (1931) and Kos (1944), referred to above, have shown them to be vegetarian, and that pollen does not necessarily always play a significant role in their diet.

Bödvarsson (1957) only repeats that, in Europe, *Bourletiella pruinosa* [= *B. signata*] lives to a great extent on the pollen of various plants; Poole's (1959) studies on the food of Collembola in a British Douglas fir plantation make passing reference to the fact that *Sminthurides aquaticus*, as reported by Macnamara (1924), will feed on conifer pollen, and that *Sminthurus viridis* will also ingest pollen [of unstated origin – he wrongly attributes the record for the latter species also to Macnamara instead of to Schött (1917) or Strebel (1932)]. Strebel and Altner (1961) indicate that the gut contents of a specimen of *Sminthurinus* [as *Sminthurus*] *aureus* (Lubbock) consisted mainly of broken-down pollen grains, that the intestine of *Heterosminthurus cornutus* Stach [= *Bourletiella bilineata* (Bourlet)] contained pollen, and that that of *Sminthurus viridis* included isolated dark brown pollen grains.

Schaller's (1962) success in culturing the 'glacier-flea' *Isotoma saltans* may have been partial because he was unable to provide the right food (? pollen). Mani (1962: 156) says that, in the Himalaya, in nearly every snow community, some species of Collembola are at the base of the pyramid of numbers and that this pyramid base includes mostly pollen and spore feeding species etc. at the snow edge. Genera mentioned are *Isotoma* Bourlet, *Proisotoma* Börner and *Hypogastrura* Bourlet (although the last is probably not a pollen feeder). The same author (p. 110) also states that wind-blown pollen grains (and spores) constitute the food of "numerous species of Collembola. . . . Vast numbers . . . come here [to the snow at elevations of 4000 m] for feeding on the wind-blown derelicts . . . including truly immense quantities of pollen grains, spores. . . . Many species of Collembola feed on the pollen grains of juniper [*Juniperus* (Coniferae, Cupressaceae)] and other plants scattered on the snow surface". Sharma and Kevan (1963) refer again very briefly to the known pollen-feeding habits of the 'glacier-fleas', *Isotoma saltans* and *I. kosiana*.

Results of an investigation of the digestion of conifer pollen grains by a collembolan, *Onychiurus pseudofimetarius* Folsom, are reported from Florida by Scott and Stojanovitch (1963). Pollen of *Juniperus pachyphloea* Torrey (Cupressaceae) was found in the gut of this species, but it is not stated whether the animal fed directly on juniper flowers; we assume not. It was concluded, either that the exines of the pollen grains were penetrated by the digestive enzymes, or that the exine of each grain was burst by the intestine in response to moisture. This occurred at or just before the cardiac valve. The intines were attacked at the mid gut, the inner ones approximately at the position of abdominal segments II and III, and the outer ones about on a level with the middle of segment III. Exines were broken up just before the pyloric valve. This investigation thus confirms that one species of collembolan, at least, can digest as well as ingest pollen, although there are indeed several previous reports of broken pollen grains in collembolan intestines (see above).

In his review of the bionomics of Collembola, Christiansen (1964) states that spores and pollen grains make up a large portion of the diet of surface-dwelling species (*cf.* Gisin, 1948). He ranks the various items of diet in several groups in a tentative order of frequency of occurrence. "*Pollen grains*, unicellular algae and spores" (most pigmented Entomobryinae) are listed second after "fungal hyphae, bacteria, dead and decaying plants and grass"; "*pollen grains*, spores and live plant material" (most sminthurids) are ranked third [our italics]. Sharma (1964, 1967) notes that pollen grains probably do not constitute a large part of the diet of *Tomocerus vulgaris* Tullberg, but coniferous pollen was frequently found in field-collected specimens (Sharma, 1964).

Brauns (1968) notes briefly again that the 'glacier-flea', *Isotoma saltans*, feeds on detritus particles and, above all, on conifer pollen deposited on ice and snow; the same is implied for the 'snow-flea', *Hypogastrura socialis* Uzel, although this may merely be an assumption. Mani (1968: 69, 70, 91) merely repeats his earlier remarks already quoted (Mani, 1962) on pollen feeding by high altitude Collembola. Walters (1968) notes that *Sminthurus viridis* will feed readily on the pollen of macrophytes. In the Canadian High Arctic, Hocking (1968) recorded in 1963, a species of collembolan "hidden in" the flowers of *Cerastium arcticum* Lange (Caryophyllaceae) at Hazen Camp, northern Ellesmere Island (see below), and *Isotoma viridis* (Bourlet) associated with those of *Saxifraga hirculus* Linnaeus (Saxifragaceae) at Resolute Bay, Cornwallis Island.

De Bernardi and Parisi (1969) mention that *Orchesella bifasciata* Nicolet includes small quantities of pollen in its diet and give a table showing quantitative estimates of the rather small proportion of the gut contents that are made up of pollen grains in that species and in *O. quinquefasciata* Bourlet, *O. villosa* (Geoffroy), *Tomocerus minor* Lubbock and *T. flavescens* Tullberg; *O. quinquefasciata* contained most, and *T. minor* least. They also discuss the topic briefly and suggest that *O. quinquefasciata* contained more pollen grains (and blue-green algae) than other species of *Orchesella* because this species, in the adult stage, is less restricted to soil; pollen grains are more important in the diet of epigeic Collembola than in that of hemiedaphic species (*cf.* Gisin, 1948). Bödvarsson (1970) has indicated that, of seven soil-inhabiting species studied, pollen grains were found very infrequently in the guts – in 3.5 per cent of *Lepidocyrtus lanuginosus* (a surface dweller), and in 1.3 per cent of *Megalothorax* [= *Neelus*] *minimum* Willem (a subterranean species).

In concluding this review of pollen feeding by Collembola, some recent unpublished observations may also be mentioned. One of us (D.K.K.) recently observed *Sminthurus viridis* [? var. *medicaginia*] on the flowers of yellow medic (*Medicago* sp., Leguminosae) in a pasture in S.E. South Australia in late winter (August), 1968, but without direct evidence of pollen feeding, although the species is reported to consume pollen. Stainer (1969), from gut examinations, found that, in spring, *Entomobryoides purpurascens* (Packard), living in wood piles in south-western Quebec, fed extensively on drifted pollen of various [deciduous] trees [mostly *Betula* spp. (Betulaceae)]. In summer they also ingested pollen, probably of ragweed [*Ambrosia trifida* Linnaeus (Compositae)] or golden-rod [*Solidago* spp. (Compositae)]. He indicated that the highest proportion of his field-collection individuals that contained pollen was 14 per cent (7 out of 50 in one sample); many samples contained none. Specimens of the same species collected by K. P. Butler under dead bark in a Red pine plantation, Kirkwood Township, Algoma District, Ontario, 6.VI.1965, also showed a few, mostly unbroken, unidentified pollen grains in the gut. Specimens of the following species collected (in pitfall traps unless stated otherwise) near Ste. Anne de Bellevue, Quebec, during May and June, 1966, by members of the McGill University Department of Entomology, also contained varying quantities of mostly unbroken, unidentified pollen: *Lepidocyrtus* sp. (immature, in *Tsuga* litter, abundant pollen), *Entomobrya clitellaria* Guthrie (under bark), *Sminthurus viridis* Linnaeus (on vegetation), *S. facialis* Banks, *Sminthurinus aureus* (Lubbock) (few grains), *S. elegans* (Fitch) (few grains) and *S. radiculus* Maynard.

Dr. J. T. Salmon (*in litt.*, 1969) writes that, in New Zealand, *Parakatianna albirubrafrons* Salmon and *P. diversitata* Salmon and their "varieties" are most common when tauhinu [*Pomaderris phylacaefolia* Loddige (Rhamnaceae)] is in flower, and, as flowers are copiously supplied with pollen, they could be pollen feeders, but he has no conclusive evidence of this; also *Polykatianna flammea* Salmon and *Pseudokatianna lutea* Salmon are taken off native New Zealand "broom" trees [presumably *Carmichaelia* spp. (Leguminosae), although *Notospartium* and *Chordospartium* spp. are also "brooms"], particularly when they are in flower, so these might also be pollen feeders. Dr. H. G. Scott (*in litt.*, 1969) has kindly supplied us with a list of species swept off vegetation, particularly conifers and grasses, in New Mexico, and it is quite likely that some of these may feed on pollen, although there is no direct evidence for this. The following were involved: *Isotoma notabilis* Schäffer, *Entomobrya assuta* Folsom, *Sinella binoculata* (Schött), *Isotobryoides ochracius* Maynard, *Lepidocyrtinus domesticus* (Nicolet), *Orchesella hexafasciata* Harvey, *O. zebra* Guthrie, *Bourletiella aquatica* Maynard, *B. arvalis* (Fitch), *B. batroches* (Wray), *B. fallonae* Maynard, *B. hortensis* (Fitch) [? = *B. signata*], *B. russata* Maynard, *B. spinata* Macgillivray and two new species of the same genus, as well as *Sminthurus obscurus* Mills, *S. fitchi* Folsom and *S. dorsalis* (Banks).

Table 1 lists alphabetically the species of Collembola recorded as visiting flowers or as ingesting pollen or both, or suspected of so doing.

Table 1. Species of Collembola recorded ingesting pollen†, visiting flowers*, or both†*, or unmarked, suspected of so doing (see text). A question mark indicates a literature record as feeding on pollen, evidence not given; (†*) indicates ingesting pollen while visiting flowers.

Bourletiella spp.†
B. aquatica Maynard
B. arvalis (Fitch)
B. batroches (Wray)
B. bilineata (Bourlet)†
B. fallonae Maynard
B. lutea (Lubbock)(†*)
B. pallipes (Bourlet)†*
B. repanda (Ågren)†*
B. russata Maynard
B. signata (Nicolet)(†*) [incl. *B. pruinosa* (Tullbert) and *B. hortensis* (Fitch)]
B. spinata Macgillivray
B. n. spp. (2)

Drepanocyrtus sp. nr. *flavovirens* (Börner)*

Entomobrya assuta Folsom†
E. clitellaria Guthrie
E. comparata Folsom(†*)
E. nivalis (Linnaeus)†* [incl. var. *immaculata* Schäffer]
E. spectabilis Reuter*

Entomobryoides purpurescens (Packard)†

Folsomia spp.†
Folsomia fimetaria (Linnaeus)(†*)

Hypogastrura spp. (?)†
Hypogastrura socialis Uzel (?)†

Isotobryoides ochracius Maynard

Isotoma spp.†
I. kosiana Bagnall† [incl. *I. nigra* Kos and *I. kosi* Paclt]
I. notabilis Schäffer
I. saltans (Nicolet)†
I. viridis (Bourlet)*

Isotomurus palustris (Miller)†

Katianna spp. (?)†

Lepidocirtinus domesticus (Nicolet)

Lepidocyrtus spp.†
L. cyaneus Tullberg†
L. lanuginosus (Gmelin)†*

Megalothorax minimum Willem†

Onychiurus pseudofimetarius Folsom†

Orchesella bifasciata Nicolet†
O. hexafasciata Harvey
O. quinquefasciata Bourlet†
O. villosa (Geoffroy)†
O. zebra Guthrie

Parakatianna spp. (?)†
P. albirubrafrons Salmon
P. diversitata Salmon

Polykatianna flammea Salmon

Proisotoma spp. (?)†

Pseudokatianna lutea Salmon

Sinella binoculata (Schött)

Sminthurides aquaticus (Bourlet)†
S. pumilis (Krausbauer) [inference only]

Sminthurinus aureus (Lubbock)†
S. elegans (Fitch)†
S. radiculus Maynard†

Sminthurus spp.†
S. dorsalis (Banks)†
S. facialis Banks†
S. fitchi Maynard
S. obscurus Mills
S. viridis (Linnaeus)†* [incl. var. *medicaginis* Schött]

Tomocerus vulgaris Tullberg†
T. flavescens Tullberg†
T. minor Lubbock†

Undetermined (2 spp.)*

Pollen as food

Faegri and Pijl (1966: 50) state that there is good reason to consider pollen as the original attractant for insects to flowers. Pollen is eaten by some beetles, bees, and flies as well as by Collembola. The chemical composition of pollen has been studied particularly in reference to the nutrition of honey-bees (Haydak, 1970). Lunden (1954) and Lubliner-Mianowska (1956) have reviewed the literature on aspects of pollen chemistry, the former author including works on allergens.

Protein content of pollens varies from 8.67 to 45.37 per cent (Lubliner-Mianowska, 1956) and averages over 25 per cent (Lunden, 1954). Conifer pollen, a well documented collembolan food, is low in protein content at about 16 per cent. The essential amino-acids in pollen show less variation (*cf.* Auclair and Jamieson, 1948; Weaver and Kuiken, 1951; Lunden, 1954). Todd and Bretherick (1942) found that carbohydrates (sugars and starches) make up about 25 per cent of pollen extracts. Lipids and other ether-extractable materials are in very variable amounts, ranging from 1 to 20 per cent (Hügel, 1962), with a mean of about 5 per cent. Interestingly, pollens of Cruciferae (*Brassica* spp.) – see below – and Compositae (*Taraxacum* sp.) are rich in lipids (Todd and Bretherick, 1942). The vitamins in pollen are diverse and in different concentrations (Lunden, 1954). Other pollen constituents reported by the above authors are pigments, enzymes, co-enzymes, and minerals, as well as undetermined materials or ash. Clearly pollen is a highly valuable food, not only for its protein content, but for all the basic nutrients for any animal able to use it.

OBSERVATIONS ON COLLEMBOLA AND FLOWERS IN THE CANADIAN HIGH ARCTIC

Although there are several records of Collembola from the arctic regions of Canada, only one (Hocking, 1968), already mentioned, has relevance in their association with flowers or pollen.

During the summers of 1967 and 1968 Collembola were collected (by P. G. K.) from the corollas of two species of flowers mostly near Hazen Camp (81° 49' N., 71° 18' W.), Ellesmere Island, District of Franklin, North West Territories. The general ecology of this area has been described by Savile (1964), who divided it by a grid used here to give precise localities within the area.

On 16 June, 1969, a single specimen of an unidentified dark species was taken from within the corolla of a flower of *Saxifraga oppositifolia* Linnaeus (Saxifragaceae). More interesting are the 20 observations and collections of *Entomobrya comparata* Folsom, within the yellow corollas of *Lesquerella arctica* (Wormskjöld) S. Watson (Cruficerae). *E. comparata* is a widespread arctic and alpine species showing much geographic polymorphism. The form here referred to is virtually restricted to arctic tundra zones (Dr. K. Christiansen, *in litt.*, 1970).

On 3 July, 1967, five specimens were collected. They were all deep in the corollas, at the base of the gynoecium and near the nectaries at the bases of the petals. This collection was made along the shore of Lake Hazen, in square L13 (Savile, 1964) (about 1 km from Hazen Camp). On the same day one other specimen was collected in square C14 (along the west bank of Blister Creek some 3.5 km from camp) in exactly the same circumstances. No further collection or observation was made, despite searching, until 16 July when two specimens were collected, again from deep within the same species of flower growing along the lake shore to the west of Gilman Camp (*ca.* 81° 54' N., 69° 30' W.), some 40 km east of Hazen Camp. On both occasions in 1967 the weather was heavily overcast.

On 3 July, 1968, at 10:30 hours Eastern Standard Time, at Hazen Camp itself (N11), two specimens of this collembolan were observed and photographed on a single plant of the same species, but within different flowers. They were watched through a 20X hand-lens as they appeared to feed directly from the dehisced anthers of the flowers. Each was observed within the same flower for more than 15 minutes, during which time they moved about on the anthers. One moved from one anther to another, crawling down the filament of one, and up on to the anther of the adjacent stamen. Whilst on the anthers, the postures of the animals did not change. Fig. 1 shows, left, how they held on with all six feet, their abdomens loosely curled over the surface of the anther but not appressed to it; and right, a specimen using the style for support; this posture was seen only once. The collembolans continually waved their antennae, again curved over the surface of the anther which they frequently touched. Their mouthparts were seen to be applied to the surface of the anther, but it was impossible to determine for certain that they were ingesting pollen grains. The assumption that they were doing so has been verified by subsequent examinations of the gut contents of the specimens observed. On this same sunny day, one further specimen was collected from another *Lesquerella* flower in the same area. On the next day, 4 July, one specimen was observed in a flower 2.5 km northeast of camp (T3). On 5 July, six specimens were collected, two more closely observed on anthers as in Fig. 1, and others seen in various parts of the Hazen Camp area. Of the six taken, three were collected from the same flowering stalk, two from within the same flower.

Fifteen specimens were sent to the Lyman Entomological Museum, Macdonald Campus, McGill University, for identification. Microscopic examination of all gut contents revealed spherical pollen grains, agreeing exactly with photomicrographs of *Lesquerella arctica* pollen. The pollen grains had been swallowed whole (a feat akin to our swallowing tennis balls!), as is reported by several authors for other pollen-feeding Collembola. Presumably these Collembola digest the nutrient-rich protoplast by diffusion through the thin micropylar membranes, as do bee larvae (Whitcomb and Wilson, 1929; Faegri, 1962), Syrphidae (Müller, 1873: 35-36; Kevan, 1970) and *Pogonomyioides segnis* (Hucket *nec* Holmgren) (Muscidae) (Kevan, 1970).

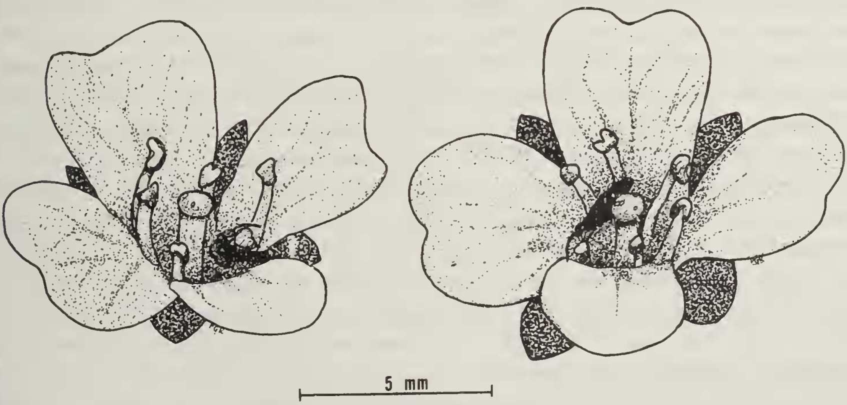

Figure 1. *Entomobrya comparata* feeding on pollen from the anthers of *Lesquerella arctica*. Left, usual position curled around an anther. Right, using style for support. Redrawn from photographs: contrast enhanced.

Entomobrya comparata has not been found, so far, in any other species than *Lesquerella arctica*, and there only around Lake Hazen; neither was it observed at any time on the ground in the vicinity of the plants, nor on their green parts. The activity occurred over a very limited period of time: for one day only in 1967, and over a three-day period in 1968. At Gilman Camp, the single record is for July 16, 1967. This short spell, the small size, and the colour match reduce the chances of observing this activity. Such an activity can be regarded as occurring within a "sensitive period" of their life cycles (Shelford, 1963: 8-9). In Shelford's words, "Sensitive periods sometimes last only a few days and may be difficult to detect. However, the identification of these sensitive periods in the life cycles of both plants and animals and the factors that affect them is very important for understanding their distribution, seasonal occurrence, and abundance". He also writes: "The activity or vital process which takes place within the narrowest environmental limits is usually the most important ecological feature of a life cycle".

Thus, the activity of these collembolans within the flowers of *L. arctica* may be extremely important to their life history. Pollen feeding may be important for nutrition, particularly for the maturation of eggs. Possibly some of the specimens were also feeding on nectar, the sugars of which could provide fuel for prolonged activity. Although Collembola have never been reported to feed on nectar, such a possibility is not precluded for, in the present case, they were found near the nectaries.

DISCUSSION

Attraction of Collembola to Flowers

Carl's (1901) suggestion, that *Bourletiella lutea* seeks refuge from the cold by inhabiting the woolly involucres of high alpine Compositae, particularly *Leodonton taraxaci*, may have some validity, for Tikhomirov *et al.* (1960) have demonstrated that elevated temperatures occur within the involucres of *Novosieversia glacialis* (Adams) F. Bolle (Rosaceae) in the Yakutsk A.S.R. in the Soviet Arctic. Similarly, the densely pubescent catkins of *Salix* spp. (Salicaceae) become considerably warmed in sunshine (Krog, 1955; Büdel, 1957; Kevan, 1970). Büdel (1956, 1959a, b) considers the microclimate within a variety of flowers with particular reference to nectar secretion (review in Hodgson, 1961), and Hocking and Sharplin (1961) consider elevated temperatures in Arctic flowers as important to insects basking within the corollas.

With regard to flowers known to be visited by Collembola, Knuth (1906, 1: 101-103) considered that some flowers offer shelter to insects during rain and at night, and among these flowers he mentions both *Campanula* and *Taraxacum*. Büdel (1959a, b) and Shamurin (1966) investigated *Taraxacum* spp. and found them to be considerably warmer under sunny conditions than under overcast conditions, and colder than the ambient air at night – by 3 C (Büdel, 1959b) – when the inflorescence had closed; yet it was this very closing which Knuth postulated would trap heat. Kevan (1970) measured temperatures within the corollas of *Lesquerella arctica* in sunshine and found that the mean temperature elevations above ambient air at the same level were 1.7 C and 1.5 C for 20 and 25 flowers at ambient air temperatures of 7.9 and 18.4 C respectively. *Cerastium alpinum* L. also has elevated temperatures within the corollas during sunshine, but this is lost under heavily overcast skies (Hocking, 1968; Kevan, 1970). The same is true of *Lesquerella arctica*, which shows a slight epinastic closing response in dim light. Kevan also made measurements and found elevated temperatures within the bowl-shaped corollas of several other species of arctic flowers. No doubt an investigation of the European *Ranunculus glacialis*, which is known to harbour Collembola would produce similar results. Among zygomorphic flowers, the legume, *Anthyllis vulneraria*, another European species in which Collembola have been found, probably also develops a considerably warmer environment with its corollas in sunshine as a result of a "greenhouse" effect such as occurs in *Pedicularis* spp. (Scrophulariaceae) (Kevan, 1970).

Of interest, also, in the association between Collembola and flowers, is the possible cryptic nature of the coloration of most flower-visiting Collembola. Table 2 shows the colours of Collembola and of flowers known to be visited by them. Information on ultra-violet reflection within the insect visual spectrum is inferred from, or given by, Kevan (1970). Data on ultra-violet reflections from a few Lepidoptera and spiders (Thomisidae) (*cf.* Lutz, 1924, 1933; Eisner *et al.*, 1969) are available, but there is nothing, unfortunately, on Collembola.

Of the 14 species of Collembola reported to occur in association with flowers, 10 are known to be light (white to yellow-green) and only three, including those from high altitudes and high latitudes, to be dark in colour. Rapoport (1969), however, indicates that Collembola from such localities are, in general, darker than those from warmer habitats. Of the 10 light-coloured species, only one, the soil-inhabiting *Folsomia fimetaria,* was reported in dark flowers, and then only in the ground-level flowers of *Aspidistra elatior*, where no colour correlation should be inferred. Eight of the remaining nine light species were recorded from white or yellow (with or without ultra-violet) flowers growing in the open; the ninth was recorded from greenhouses, probably on light-coloured flowers.

There is thus a strong suggestion that light-coloured Collembola visiting exposed flowers prefer those in which they are least conspicuous. Objections to this suggestion could, however, be raised because the relative abundance of dark and light Collembola and flowers within the range of cohabitation of each is not known (see also Rapoport, 1969).

The three dark species visiting flowers show little or no comparable association with dark flowers; only one (unidentified) species was collected from the dark (purple) flowers of *Saxifraga oppositifolia*, which had a colour saturation of only about 50 per cent within the insect visual spectrum (Kevan, 1970). The others are recorded from white and/or yellow (± ultra-violet) flowers, although, interestingly enough, one of them, *Bourletiella signata*, occurred also in the light blue (probably without ultra-violet) flowers of *Campanula barbata.*

Brief résumés on sensory perception in Collembola are given by Denis (1949) and Paclt (1956), but the greater part of what is known is due to Strebel (1932), who made experimental observations on the reactions of various species of Collembola to light, temperature, smell, taste, and touch. If the suggestion that Collembola select flowers in which they are inconspicuous is valid, colour vision might be expected, but there is no direct evidence for this in the literature.

Most of the flowers listed as being visited by Collembola are relatively conspicuous, but they also produce scent and nectar as well as pollen. Those of *Lesquerella arctica* are no exception. Although not large (*ca.* 1 cm in diameter), they, too, are brightly coloured (yellow without ultra-violet), and produce scent, nectar, and pollen. A sense of smell was indicated for Collembola by Handschin (1926) and Ripper (1930), on account of their retreat from repellent volatile substances. Strebel (1932) observed, in several species, reactions towards or away from odours, the main sensory region (in *Tomocerus minor*) being on the antennae. He concluded, however, that the sense of smell does not play a significant role in the location of food. There is no evidence that scent attracts Collembola to flowers. Taste is apparently well developed in Collembola according to Strebel but, from his observations, sweet substances neither attract nor repel them. Thus there is again no evidence that nectar attracts Collembola to flowers.

Strebel's (1932) experiments on temperature reactions were confined to *Hypogastrura purpurascens* Lubbock, in which he indicated sensitivity to both warmth and cold. The sensory regions were found to be located mainly on the antennae and the posterior part of the abdomen. Strebel also indicates that warmth overcame negative phototaxis. The

Table 2. Colour correlation between species of Collembola and flowers visited by them.

Species of Collembola	Colour	Flowers of –	Colour
Bourletiella lutea	Yellow, white below	*Anthyllis vulneraria*	Rosy white – yellow
		Leontodon taraxaci [= *L. montanus*] (involucres only)	Yellow (involucres grey-green)
		Ranunculus glacialis	White, yellow centre and androecium
B. pallipes	Black-violet, yellow face, appendages and maculae	*Ranunculus glacialis*	White, yellow centre and androecium
B. repanda	Yellow	*Ranunculus glacialis*	White, yellow centre and androecium
B. signata [incl. *B. hortensis* and *B. pruinosa*]	Variable, black- to green-violet, head partly yellowish	*Ranunculus glacialis*	White, yellow centre and androecium
		Taraxacum sp.	Yellow (probably UV distally on rays)
		Campanula barbata	Pale blue
Drepanocyrtus sp. [nr. *D. flavovirens*]	? Yellow-green	*Coffea* sp.	White, yellow androecium
Entomobrya nivalis ab. *immaculata*	Pale yellow	*Anthyllis vulneraria*	Rosy white – yellow
E. spectabilis	Yellow, variegated	Orchidaceae	? (some yellow?)
E. comparata	Yellow	*Lesquerella arctica*	Yellow (no UV)
*Folsomia fimetaria**	White*	*Aspidistra elatior**	Purplish and greenish*
Isotoma viridis	Variable. Yellowish, usually dull yellow-green, sometimes grey-green, reddish or bluish	*Saxifraga hirculus*	Yellow (UV distally)
Lepidocyrtus lanuginosus	Yellow-white to brown-red	*Ranunculus glacialis*	White, yellow centre and androecium
Sminthurus viridis [? var. *medicaginis*]	Yellow-green	*Medicago* sp.	Yellow
Unidentified	Unknown	*Cerastium arcticum*	White, pale yellow androecium (no UV)
Unidentified	Blackish	*Saxifraga oppositifolia*	Purple (no UV)

*Flowers hidden at soil level; visiting species soil inhabiting; presumably no colour correlation involved.

ameliorated microclimate within the flowers of *Lesquerella arctica* may or may not serve to hold *Entomobrya comparata* (which is not a negatively phototactic species), for it was found in the corollas on both overcast and sunny days. However, Collembola in an ameliorated thermal regime, such as that provided by flower corollas, would metabolize more rapidly and be more active, and this would surely be advantageous in arctic and alpine regions of low heat budget.

Lesquerella arctica grows in dry sandy places around Lake Hazen. The plant is decumbent, its flowers held upright about 1 cm above the ground. Thus a combination of attractants, cryptic protection, accessibility, and perhaps cohabitation, make for the relationship in the High Arctic between this plant and *Entomobrya comparata*. This collembolan was not found in flowers of any other species growing in the vicinity of *L. arctica*, nor, for that matter, anywhere else.

Collembola as Pollinators

Handschin (1924) believed there was a relationship between *Bourletiella lutea* and *Ranunculus glacialis*. He concluded that the Collembola seek out the flowers in order to obtain nourishment from their reproductive organs. From the observations on *Entomobrya comparata* in the flowers of *Lesquerella arctica*, a similar relationship is postulated in respect of the "sensitive period" in the life of this collembolan. Handschin left open the question of pollination by *Bourletiella lutea*, but Strebel (1932) suggested that *Folsomia fimetaria* might be a pollinator of *Aspidistra elatior*. Kevan (1970), however, found that *L. arctica* is independent of arthropods for pollination, although some cross-pollination by arthropods may occur.

The behaviour and probably the size of *E. comparata* precludes these collembolans from being effective pollinators, even within a single flower, although pollen grains do adhere to their hairy bodies. Arthropods as small as Collembola would have no cause to visit more than one flower within the period of viability of any pollen they might carry on their bodies, so that, even if they did occasionally effect cross-pollination, this would be fortuitous.

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